DISCRETE-TIME NONLINEAR PAIR FORMATION MODELS WITH GEOMETRIC SOLUTIONS

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Abstract: Extensions of the discrete Malthus model are carried out to include males, females, and various forms of mating. The resulting discrete nonlinear homogeneous pair-formation model parallels those of Kendall [24], Keyfitz [25], Fredrickson [11], Pollard [36] and *Hadeler et al.*'s [13-18]. The analysis of Hadeler *et al.* goes through even when the mating function depends on the number of females or males in pairs. Extensions are discussed.

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1. Introduction

The discrete-time analogue of the Malthus model is given by

$$P(t+1) = \lambda P(t), \qquad P(0) = P_0, \qquad (DM)$$

where $P(t)$ is the population at generation t and λ is the multiplicative growth factor per generation [28, 30-32]. The solution of Equation (DM) is $P(t) = \lambda^t P_0$. Hence, for the initial population size $P_0 > 0$ the model predicts unbounded geometric growth if $\lambda > 1$; geometric decline to extinction if $\lambda < 1$; and no growth ($P(t) = P_0$) if $\lambda = 1$.

Hence, the Malthus model predicts population explosion in the simplest possible situation and it implicitly follows the population of females. Two-sex models with various mating strategies have been developed but mostly at the level of the gene (see Crow and Kimura [10]). The fact that genetic models do not explicitly incorporate individuals allows for the study of the impact of various mating systems on the gene (genotype and phenotype) frequencies of a population. Developing useful mating models at the level of the individual has proved difficult. Nevertheless, successful first-level approaches have been developed for continuous-time models by Kendall [24], Keyfitz [25], McFarland [33], Fredrickson [11], Pollard [36], Hoppensteadt [19], and more recently by Castillo-Chavez *et al.* [2-8], Caswell [9], Hadeler *et al.* [13-18], Hsu [20-23], Martcheva [29]; to name a few). Analogue stochastic pair-formation models have also been developed (see Luo *et al.* [27])

In this article we extend the continuous-time pair formation models of Kendall [24], Keyfitz [25], Fredrickson [11], Pollard [36] and Hadeler *et al.'s* [13-18] to populations with discrete non-overlapping generations. Specifically, we expand the discrete-time Malthus model into a nonlinear homogeneous model that includes males, females, and couples. This discrete-time pair-formation model is capable of supporting geometric solutions, and hence, it can be extended to heterogeneous mixing populations that support stable pair distributions (see Castillo-Chavez *et al.* [6,7], Luo *et al.* [27]).

The study of pair-formation for humans has a long history and has been driven to a great degree by demographers. We are all aware of the changes that have taken place over the last decades on the stability of relationships. Hence, the process of pair-formation and dissolution have become central to demography in the context of populations with overlapping generations. Data on the process of pair-formation and dissolution for populations with discrete non-overlapping generations is also extensive. For example, the rates of pair-formation and dissolution for the population of Corsican blue tits (*Parus caeruleus*), have been extensively studied under all sorts of conditions and a myriad of questions have been raised regarding their impact on the population dynamics as well as their evolutionary origin [1]. For a detail account see [1] and the reference therein.

The paper is organized as follows: Section 2 introduces the basic two-sex discrete-time model with non-overlapping generations; Sections 3 explores the possibilities of constant solutions and sets conditions for the existence of geometric solutions; Section 4 establishes conditions for the stability of geometric solutions; Section 5 gives an illustrative example; Section 6 discusses some of the implications of our work and outlines some future work.

2. Homogeneous Discrete-Time Pair-Formation Model

At generation t, we let $x(t)$ denote the population size of single females; $y(t)$ denote the population size of single males; $p(t)$ denote the population size of pairs (couples); $p_x(t)$ denote the population size of coupled females; and $p_y(t)$ denote the population size of coupled males. We further assume sequential monogamy, that is, $p(t) = p_x(t) = p_y(t)$ and that the total population size at generation t, $T(t)$, is given by $T(t) \equiv x(t) + y(t) + 2p(t)$. Furthermore, the model is built assuming an implicit sequential process which is typical of many discrete-time models (see Caswell [9]) but not essential. However, its use clarifies the underlying modeling assumptions and facilitates future extensions. Hence, it is assumed that survival of females (μ_x), males (μ_y) or pairs ($\mu_x\mu_y$) is required before reproduction, pair-formation, and pair-dissolution ($0 \leq \mu_x, \mu_y \leq 1$). This order gives rise to a transparent and simple governing equation for the dynamics of the total population as it will be shown below. At the end of each generation, new females [respectively, males] are born, from the pairs, at the per-capita production rate of β_x [respectively, β_y] per generation; the fraction $(1 - \mu_x)$ [respectively, $(1 - \mu_y)$] of females [respectively, males] are removed (death or retirement from mating activities); and, it is assumed that couples separate independently with probability $(1-\sigma)$.

The populations of single females and single males increase by the death of a partner (widows become single), separation of couples ("divorcees" become single) or birth (delay in recruitment is not assumed). Individuals are removed from the single classes by mating (pair-formation), pair-dissolution, or death. The functions $G : [0,\infty) \times [0,\infty) \times [0,\infty) \to [0,1]$ and $H : [0,\infty) \times [0,\infty) \times [0,\infty) \to [0,1]$ denote the state-dependent probability functions that model the likelihood of not having a successful interaction (that is, an interaction that results in the creation of a heterosexual pair) given that you had a contact with a potential partner, that is, a single female (if you are a male) or a single male (if you are a female). Hence, G and H are functions of the population vectors at generation t, $(x(t), y(t), p(t))$. The pair-formation (marriage) function, a function of the population vectors $(x(t), y(t), p(t))$, is denoted by $\phi : [0,\infty) \times [0,\infty) \times [0,\infty) \to [0,\infty)$. Fredrickson [11], Hadeler et al.[13-18], Kendall [24], Keyfitz [25], McFarland [33] and Pollard [36] have proposed various functional forms of ϕ that satisfy the following properties (and a few more) for all $(x(t), y(t), p(t)) \in [0,\infty) \times [0,\infty) \times [0,\infty)$; $u(t), v(t), w(t) \geq 0$; and $k \in [0,\infty)$:

(i)

$$\phi(x(t), y(t), p(t)) \geq 0,$$

(ii)

$$\phi(x(t)+u(t), y(t)+v(t), p(t)+w(t)) \geq \phi(x(t), y(t), p(t)), \;\; for \; u(t), v(t), w(t) \geq 0,$$

(iii)

$$\phi(kx(t), ky(t), kp(t)) = k\phi(x(t), y(t), p(t)),$$

(iv)

$$\phi(x(t), 0, p(t)) = \phi(0, y(t), p(t)) = 0.$$

We assume that at least properties (i), (ii) and (iii) for ϕ are satisfied throughout. Our assumptions and definitions lead to the following discrete-time pair-formation nonlinear homogeneous model:

$$\left.\begin{array}{rcl} x(t+1) & = & (\beta_x\mu_x\mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p(t) + \mu_x x(t)G(x(t), y(t), p(t)), \\ y(t+1) & = & (\beta_y\mu_y\mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p(t) + \mu_y y(t)H(x(t), y(t), p(t)), \\ p_x(t+1) & = & \sigma\mu_x\mu_y p(t) + \mu_x x(t)(1 - G(x(t), y(t), p(t))), \\ p_y(t+1) & = & \sigma\mu_x\mu_y p(t) + \mu_y y(t)(1 - H(x(t), y(t), p(t))), \end{array}\right\} \quad (1)$$

where $p(t{+}1) = p_x(t{+}1) = p_y(t{+}1)$. In other words, the last equation is redundant. We have sequential monogamy provided that the total rates of pair-formation of males and females per-generation match. Hence, we assume throughout that

$$\mu_x x(t)(1-G(x(t), y(t), p(t))) = \mu_y y(t)(1-H(x(t), y(t), p(t))) \equiv \phi(x(t), y(t), p(t)). \quad (*)$$

Property (*) implies that the specification of the probability function G prescribes H and ϕ implicitly, provided that steps are taken to guarantee that $0 \leq H(x(t), y(t), p(t)) \leq 1$, otherwise the system may exhibit negative solutions (a "negative" number of pairs in at least some generations).

Meeting property (*) is important here and follows from having a uniform modelling policy for all processes, in other words, if you are a single female, then there is a probability G of remaining single and $1 - G$ of finding a partner per-generation. Furthermore, the probabilities are in general different for males and females. If G is given then $1-G$ is fixed and (*) fixes H and $1-H$. Of course, both functions could change from generation to generation as long as (*) is satisfied. Here, we have chosen some simple examples where one of the functions is fixed a priori.

From System (1), with both $0 \leq G(x(t), y(t), p(t)) \leq 1$ and $0 \leq H(x(t), y(t), p(t)) \leq 1$, one sees that $T(t)$ obeys the equation

$$T(t+1) = (\beta_x \mu_x \mu_y + \beta_y \mu_y \mu_x + \mu_x + \mu_y)p(t) + \mu_x x(t) + \mu_y y(t).$$

Hence, whenever the females and males have the same survival probability [that is, if $\mu = \mu_x = \mu_y$] $T(t)$ satisfy

$$T(t+1) \equiv (\beta_x + \beta_y)\mu^2 p(t) + \mu T(t),$$

where individuals either die or survive and reproduce. This last equation suggests extensions with prescribed (or unknown) population dynamics that are independent of the population of singles.

If the probability function $G(x(t), y(t), p(t))$ is given, then $H(x(t), y(t), p(t))$ and $\phi(x(t), y(t), p(t))$ are determined by property (*). In fact,

$$H(x(t), y(t), p(t)) = 1 - \frac{\mu_x x(t)(1 - G(x(t), y(t), p(t)))}{\mu_y y(t)},$$

and

$$\phi(x(t), y(t), p(t)) = \mu_x x(t)(1 - G(x(t), y(t), p(t))),$$

where we focus on solutions $(x(t), y(t), p(t))$ that belong to the set Ω, where

$$\Omega := \{(x(t), y(t), p(t)) \mid 0 \le \frac{x(t)}{y(t)} \le \frac{\mu_y}{\mu_x(1 - G(x(t), y(t), p(t)))}\}$$

to guarantee that $0 \le H(x(t), y(t), p(t)) \le 1$. Furthermore, our homogeneity assumption implies that the set Ω is positively invariant on the set of geometric solutions of System (1), provided that the initial conditions are in Ω.

If for example

$$G(x(t), y(t), p(t)) = \frac{p(t)}{\epsilon x(t) + y(t) + p(t)}$$

where the constant $\epsilon \in [0, 1]$, is a measure of interference competition between females, then

$$H(x(t), y(t), p(t)) = 1 - \frac{\mu_x x(t)(\epsilon x(t) + y(t))}{\mu_y y(t)(\epsilon x(t) + y(t) + p(t))} \text{ and}$$

$$\phi(x(t),y(t),p(t)) \equiv \frac{\mu_x x(t)(\epsilon x(t)+y(t))}{\epsilon x(t)+y(t)+p(t)},$$

provided $(x(t),y(t),p(t))$ belong to the set

$$\Omega := \{(x(t),y(t),p(t)) \mid 0 \leq \frac{x(t)}{y(t)} \leq \frac{\mu_y(\epsilon x(t)+y(t)+p(t))}{\mu_x(\epsilon x(t)+y(t))}\}.$$

3. Preliminary Analysis

If we let $(x(t),y(t),p(t)) = (x,y,p)$ in $\mathbb{R}^3_+$, then the reproduction function of System (1) is given by the map $F : \mathbb{R}^3_+ \to \mathbb{R}^3_+$ defined by $F(x,y,p) =$

$$\begin{bmatrix} (\beta_x\mu_x\mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p + \mu_x x G(x,y,p) \\ (\beta_y\mu_y\mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p + \mu_y y H(x,y,p) \\ \sigma\mu_x\mu_y p + \mu_x x(1-G(x,y,p)) \end{bmatrix},$$

where $1 - G(x,y,p) \geq 0$. F^t is the map F composed with itself t times, and $F^t_i(x,y,p)$ is the i^{th} component of F^t evaluated at the point (x,y,p) . Therefore, F^t gives the population densities in generation t. The set of iterates of the map F is therefore equivalent to the set of all density sequences generated by System (1).

The fixed points of F satisfy the equation $F(x,y,p) = (x,y,p)$. That is,

$$
\begin{aligned}
(\beta_x\mu_x\mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p - x + \mu_x x G(x,y,p) &= 0 \qquad (2)\\
(\beta_y\mu_y\mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p - y + \mu_y y H(x,y,p) &= 0 \qquad (3)\\
-p + \sigma\mu_x\mu_y p + \mu_x x - \mu_x x G(x,y,p) &= 0 \qquad (4)
\end{aligned}
$$

Using Equation (2), (3) and (4) together with the fact that $\mu_x x(t)(1-G(x(t),y(t),p(t))) = \mu_y y(t)(1-H(x(t),y(t),p(t)))$ we obtain that

$$
\left.\begin{aligned}
\tfrac{x}{p} &= \tfrac{\beta_x\mu_x\mu_y+\mu_x-1}{1-\mu_x},\\
\tfrac{y}{p} &= \tfrac{\beta_y\mu_y\mu_x+\mu_y-1}{1-\mu_y}.
\end{aligned}\right\} (5)
$$

Equation (4) implies that $\phi(x,y,p) = p(1-\sigma\mu_x\mu_y)$. Consequently, System (5) and the homogeneity condition on ϕ imply that

$$
(1-\sigma\mu_x\mu_y)p = p\phi(\frac{\beta_x\mu_x\mu_y+\mu_x-1}{1-\mu_x}, \frac{\beta_y\mu_y\mu_x+\mu_y-1}{1-\mu_y}, 1). \qquad (6)
$$

Parameters in System (1) are not likely to satisfy Equation (6). Hence constant solutions rarely exist, that is, they are not generic. We therefore focus on a search for geometric solutions, that is solutions of the form

$$\left.\begin{aligned} x(t) &= \lambda^t x_0, \\ y(t) &= \lambda^t y_0, \\ p(t) &= \lambda^t p_0. \end{aligned}\right\} \quad (7)$$

Substituting (7) in System (1), leads to the following nonlinear eigenvalue problem:

$$\left.\begin{aligned} \lambda x_0 &= (\beta_x \mu_x \mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p_0 + \mu_x x_0 - \phi(x_0, y_0, p_0), \\ \lambda y_0 &= (\beta_y \mu_y \mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p_0 + \mu_y y_0 - \phi(x_0, y_0, p_0), \\ \lambda p_0 &= \sigma\mu_x\mu_y p_0 + \phi(x_0, y_0, p_0). \end{aligned}\right\} \quad (8)$$

From (8) we see that,

$$\left.\begin{aligned} \phi(x_0, y_0, p_0) &= (\beta_x \mu_x \mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p_0 + (\mu_x - \lambda)x_0, \\ \phi(x_0, y_0, p_0) &= (\beta_y \mu_y \mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p_0 + (\mu_y - \lambda)y_0, \\ \phi(x_0, y_0, p_0) &= (-\sigma\mu_x\mu_y + \lambda)p_0. \end{aligned}\right\} \quad (9)$$

It is obvious that the point $[1, 0, 0]$ is a solution of System (9) whenever $\lambda = \mu_x$ and the point $[0, 1, 0]$ is also a solution of System (9) whenever $\lambda = \mu_y$. Consequently, $[(\mu_x)^t, 0, 0]$ and $[0, (\mu_y)^t, 0]$ are the trivial geometric solutions of System (1). Since there are no pairs then the population eventually becomes extinct whenever $0 \leq \mu_x, \mu_y < 1$. We now look for nontrivial solutions, that is, solutions where $x_0 > 0, y_0 > 0$ and $p_0 > 0$. From System (9) we find that

$$\left.\begin{aligned}(-\sigma\mu_x\mu_y + \lambda)p_0 &= (\beta_x\mu_x\mu_y + (1-\mu_y)\mu_x + (1-\sigma)\mu_x\mu_y)p_0 + (\mu_x - \lambda)x_0,\\(-\sigma\mu_x\mu_y + \lambda)p_0 &= (\beta_y\mu_y\mu_x + (1-\mu_x)\mu_y + (1-\sigma)\mu_x\mu_y)p_0 + (\mu_y - \lambda)y_0.\end{aligned}\right\} \quad (10)$$

Hence,

$$\begin{cases}\frac{x_0}{p_0} &= \frac{\beta_x\mu_x\mu_y + \mu_x - \lambda}{\lambda - \mu_x}\\\frac{y_0}{p_0} &= \frac{\beta_y\mu_y\mu_x + \mu_y - \lambda}{\lambda - \mu_y},\end{cases}$$

and, $\phi(\frac{x_0}{p_0}, \frac{y_0}{p_0}, 1) = (-\sigma\mu_x\mu_y + \lambda)$. Substituting the above expressions for $\frac{x_0}{p_0}, \frac{y_0}{p_0}$ leads to the characteristic equation of System (1):

$$-\sigma\mu_x\mu_y + \lambda = \phi(\frac{\beta_x\mu_x\mu_y}{\lambda - \mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda - \mu_y} - 1, 1), \qquad (11)$$

therefore, the existence of geometric solutions depends on proving the existence of positive $\lambda-$solutions to (11) with initial condition (x_0, y_0, p_0) in the set Ω. This is established in Lemma 3.1.

Lemma 3.1. *Equation (11), the characteristic equation, has a unique real solution λ^* if and only if*

$$\mu_x < \frac{([\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)])}{2(1-\sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1-\sigma\mu_y)-(1-\beta_y\mu_y)\phi_y(1,0,0)-\phi_p(1,0,0)]^2-4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0)-\phi_y(1,0,0))}}{2(1-\sigma\mu_y)}$$

and

$$\mu_y < \frac{([\mu_x(1-\sigma\mu_x)-(1-\beta_x\mu_x)\phi_x(0,1,0)-\phi_p(0,1,0)])}{2(1-\sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1-\sigma\mu_x)-(1-\beta_x\mu_x)\phi_x(0,1,0)-\phi_p(0,1,0)]^2-4\mu_x(1-\sigma\mu_x)(\phi_p(0,1,0)-\phi_x(0,1,0))}}{2(1-\sigma\mu_x)},$$

where the discriminants $\Delta_x, \Delta_y \geq 0$.

The proof of Lemma 3.1 is in the Appendix.

4. Stability in Homogenous Systems

The matrix equation for System (1) is

$$u(t+1) = Au(t) + f(u(t)), \tag{12}$$

where

$$A = \begin{bmatrix} \mu_x & 0 & \mu_x + \beta_x \mu_x \mu_y - \sigma \mu_x \mu_y \\ 0 & \mu_y & \mu_y + \beta_y \mu_x \mu_y - \sigma \mu_x \mu_y \\ 0 & 0 & \sigma \mu_x \mu_y \end{bmatrix}, \quad u = [x, y, p]' \in \mathbb{R}^3_+ \text{ and}$$

$f(u) = [-\phi(x,y,p), -\phi(x,y,p), \phi(x,y,p)]'$ is homogeneous ($'$ = transpose).

To establish conditions for the stability of geometric solutions, we let $L(u) = x + y + 2p$ (L is a metric). Observe that $L(\lambda^t u_0) = \lambda^t(x_0 + y_0 + 2p_0) = \lambda^t L(u_0)$. The introduction of the new variable $w(t) = \frac{u(t)}{L(u(t))}$ implies that the geometric solution $u(t) = \lambda^t u_0$ correspond to $w(t) = \frac{\lambda^t u_0}{\lambda^t L(u_0)} = \frac{u_0}{L(u_0)}$, that is, to a constant solution in $\mathbb{R}^3_+$. A simple computation transforms System (12) into the following nonlinear system of equations for the new variable $w(t)$:

$$w(t+1) = \frac{Aw(t) + f(w(t))}{L(Aw(t) + f(w(t)))}. \qquad (13)$$

System (13) is a nonhomogeneous system of difference equation and its fixed points, w_∞, satisfy the equation

$$w_\infty = \frac{Aw_\infty + f(w_\infty)}{L(Aw_\infty + f(w_\infty))}$$

where $L(Aw_\infty + f(w_\infty))$ is a number (due to the homogeneity of L). Consequently, the fixed points or constant solutions of Equation (13) satisfy the nonlinear eigenvalue problem

$$\lambda^* w_\infty = A w_\infty + f(w_\infty), \qquad (14)$$

where λ^* is a constant. Equation (14) is equivalent to Equation (8).

If $u(t)$ is a solution of System (1) then $w(t)$ is a solution of System (13). Conversely, if we assume that $w(t)$ is a solution of System (13) then $u(t) = \lambda^t w(t)$ is a solution of System (1) provided that $L(Aw(t) + f(w(t)) = \lambda$. Hence, System (1) and System (13) are equivalent in the sense that if a solution to System (1) is found then a solution of the other is immediately determined. Conversely, if a solution of System (13) with $L(Aw(t) + f(w(t)) \equiv \lambda$ is found, then a solution of (1) is determined.

4.1. Stability of Nontrivial Equilibrium

We now investigate the stability of the nontrivial geometric solution $[(\lambda^*)^t x_0, (\lambda^*)^t y_0, (\lambda^*)^t p_0]$ of System (1). If we divide by $p(t)$ in System (1) and use homogeneity then $\xi(t) = \frac{x(t)}{p(t)}$, $\eta(t) = \frac{y(t)}{p(t)}$ and $\varsigma(t) = \frac{p(t)}{p(t)}$ satisfy the following equations:

$$\left.\begin{aligned}
\xi(t+1) &= \tfrac{\beta_x \mu_x \mu_y + \mu_x + \mu_x \xi(t)}{\sigma \mu_x \mu_y + \phi(\xi(t), \eta(t), 1)} - 1, \\
\eta(t+1) &= \tfrac{\beta_y \mu_x \mu_y + \mu_y + \mu_y \eta(t)}{\sigma \mu_x \mu_y + \phi(\xi(t), \eta(t), 1)} - 1, \\
\varsigma(t+1) &= 1.
\end{aligned}\right\} (15)$$

If $[\xi_0, \eta_0, 1] = [\frac{x_0}{p_0}, \frac{y_0}{p_0}, 1]$ is a positive fixed point of System (15) then the Jacobian matrix at this fixed point is $J =$

$$\begin{bmatrix} \frac{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))\mu_x-(\beta_x\mu_x\mu_y+\mu_x+\mu_x\xi_0)\phi_\xi(\xi_0,\eta_0,1)}{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))^2} & \frac{-(\beta_x\mu_x\mu_y+\mu_x+\mu_x\xi_0)\phi_\eta(\xi_0,\eta_0,1)}{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))^2} & 0 \\ \frac{-(\beta_y\mu_x\mu_y+\mu_y+\mu_y\eta_0)\phi_\xi(\xi_0,\eta_0,1)}{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))^2} & \frac{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))\mu_y-(\beta_y\mu_x\mu_y+\mu_y+\mu_y\eta_0)\phi_\eta(\xi_0,\eta_0,1)}{(\sigma\mu_x\mu_y+\phi(\xi_0,\eta_0,1))^2} & 0 \\ 0 & 0 & 0 \end{bmatrix} =$$

$$\begin{bmatrix} \frac{(1+\xi_0)(\mu_x-(1+\xi_0)\phi_\xi(\xi_0,\eta_0,1))}{\mu_x(\beta_x\mu_y+1+\xi_0)} & \frac{-(1+\xi_0)^2\phi_\eta(\xi_0,\eta_0)}{\mu_x(\beta_x\mu_y+1+\xi_0)} & 0 \\ \frac{-(1+\eta_0)^2\phi_\xi(\xi_0,\eta_0,1)}{\mu_y(\beta_y\mu_x+1+\eta_0)} & \frac{(1+\eta_0)(\mu_y-(1+\eta_0)\phi_\eta(\xi_0,\eta_0,1))}{\mu_y(\beta_y\mu_x+1+\eta_0)} & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Naturally, due to the rescaling $\lambda = 0$, is an eigenvalue of J. Applying the Jury test on the remaining 2 by 2 submatrix with nonzero entries one has that $[\xi_0, \eta_0, 1]$ is asymptotically stable provided that $| \, tra(J) \, | < 1 + \det(J) < 2$ where

$$tra(J) = \frac{(1+\xi_0)(\mu_x - (1+\xi_0)\phi_\xi(\xi_0,\eta_0,1))}{\mu_x(\beta_x\mu_y + 1 + \xi_0)} + \frac{(1+\eta_0)(\mu_y - (1+\eta_0)\phi_\eta(\xi_0,\eta_0,1))}{\mu_y(\beta_y\mu_x + 1 + \eta_0)}$$

and

$$\begin{aligned} \det(J) \quad = \quad & (\frac{(1+\xi_0)(\mu_x - (1+\xi_0)\phi_\xi(\xi_0,\eta_0,1))}{\mu_x(\beta_x\mu_y + 1 + \xi_0)})(\frac{(1+\eta_0)(\mu_y - (1+\eta_0)\phi_\eta(\xi_0,\eta_0,1))}{\mu_y(\beta_y\mu_x + 1 + \eta_0)}) - \\ & (\frac{(1+\eta_0)^2\phi_\xi(\xi_0,\eta_0,1)}{\mu_y(\beta_y\mu_x + 1 + \eta_0)})(\frac{(1+\xi_0)^2\phi_\eta(\xi_0,\eta_0,1)}{\mu_x(\beta_x\mu_y + 1 + \xi_0)}). \end{aligned}$$

4.2. Stability: Original System Versus Re-scaled System

Dividing the total population size in System (13) lead to the following nonlinear nonhomogeneous system:

$$\left.\begin{array}{l} w(t+1) = \frac{Aw(t)+f(w(t))}{L(Aw(t)+f(w(t)))} \\ L(w(t)) = 1. \end{array}\right\} (16)$$

The expression, $L(Aw(t) + f(w(t)))$, is a function of t which we denote by $\lambda(t)$. The time-independent solutions of System (13) satisfy the nonlinear eigenvalue problem

$$\left.\begin{array}{l} Aw_0 + f(w_0) = \lambda^* w_0 \\ L(w_0) = 1 \end{array}\right\} (17)$$

where $\lambda^* = L(Aw_0 + f(w_0))$. The homogeneity property of $f(z)$ implies that if z is very small (that is, z is close to zero in magnitude) then $f'(z)z \approx f(z)$. Using this approximation one arrives to the following approximate linear system (whenever w_0 is very small):

$$\left.\begin{array}{l} Aw_0 + f'(w_0)w_0 = \lambda^* w_0 \\ L(w_0) = 1, \end{array}\right\} (18)$$

where $f'(w_0)$, a 3×3 matrix, is the Jacobian matrix at w_0. Since $f'(w_0)$ is a homogeneous function of degree zero, in System (12), then $B \equiv A + f'(w_0)$ is its Jacobian matrix at w_0. Furthermore, the first equation in System (18) implies that λ^* is an eigenvalue of B with corresponding eigenvector w_0.

We take the perturbation $\chi(t) = w(t) - w_0$ in System (16) and linearize $f(w)$ around w_0. Consequently, we obtain

$$\chi(t+1) = w(t+1) - w_0 = \frac{B\chi(t) - w_0 L(B\chi(t))}{\lambda^* + L(B\chi(t))}.$$

From the above discussion, one finds the linearization of the right-hand-side of System (16) to be

$$\chi(t+1) = \frac{B\chi(t) - w_0 L(B\chi(t))}{\lambda^* + L(B\chi(t))}. \qquad (19)$$

The Jacobian matrix of System (16), $J(w_0)\chi(t)$ is therefore given by

$$J(w_0)\chi(t) = \frac{B\chi(t) - w_0 L(B\chi(t))}{\lambda^* + L(B\chi(t))}. \qquad (20)$$

Therefore, $\chi(t) \to 0$ as $t \to \infty$ provided that all the eigenvalues of $J(w_0)$ are less than one in absolute value. Now, we relate the condition that all the eigenvalues of $J(w_0)$ are less than one in absolute value to an equivalent condition for the matrix B. These results are stated in the next theorem and its corollary.

Theorem 4.1. *If $\lambda \neq \lambda^*$ is an eigenvalue of B corresponding to an eigenvector v, then $\frac{\lambda}{2\lambda^*-\lambda}$ is an eigenvalue of $J(w_0)$ corresponding to an eigenvector $V = w_0 - v$ [that is, $J(w_0)V = \frac{\lambda}{\lambda^*+L(BV)}V$, where $V = w_0 - v$]. Conversely, if $\lambda \neq \frac{\lambda^*}{\lambda^*+L(BV)}$ is an eigenvalue of $J(w_0)$ with corresponding eigenvector V, then $\lambda(\lambda^*+L(BV))$ is an eigenvalue of B corresponding to an eigenvector $v = V + \frac{1}{\lambda(\lambda^*+L(BV))-\lambda^*} w_0 L(BV)$.*

The proof of Theorem 4.1 is in the Appendix. The proof of Corollary 4.2 is immediate and is omitted.

Corollary 4.2. *The geometric solution with positive geometric ratio λ^* is stable if λ^* is a simple eigenvalue of B and*

$$0 < \lambda < \lambda^* \text{ for all eigenvalues } \lambda \text{ of } B$$

and unstable if

$$\lambda > \lambda^* \text{ for some eigenvalue } \lambda \text{ of } B.$$

5. Stability of Trivial Solutions

Here, we use the stability criteria of the previous section to determine the stability of trivial equilibrium solutions. Recall that $[1, 0, 0]$ is a trivial solution of System (9).

Notice that

$$\begin{aligned} \phi_x(1,0,0) &= \lim_{h\to 0} \tfrac{\phi(1+h,0,0)-\phi(1,0,0)}{h} \\ &= \lim_{h\to 0} \tfrac{(1+h-1)\phi(1,0,0)}{h} \\ &= \lim_{h\to 0} \phi(1,0,0) = 0. \end{aligned}$$

Consequently,

$$J([1,0,0]) = \begin{bmatrix} \mu_x - \lambda & -\phi_y(1,0,0) & \mu_x + \beta_x\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0) \\ 0 & \mu_y - \phi_y(1,0,0) - \lambda & \mu_y + \beta_y\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0) \\ 0 & \phi_y(1,0,0) & \sigma\mu_x\mu_y + \phi_p(1,0,0) - \lambda \end{bmatrix}.$$

It is easy to see that μ_x is an eigenvalue of $J([1,0,0])$. Next, we show that if λ is any other eigenvalue of $J([1,0,0])$, then $\lambda < \mu_x$.

$$\begin{vmatrix} \mu_y - \phi_y(1,0,0) - \lambda & \mu_y + \beta_y\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0) \\ \phi_y(1,0,0) & \sigma\mu_x\mu_y + \phi_p(1,0,0) - \lambda \end{vmatrix} =$$

$$(\mu_y - \phi_y(1,0,0) - \lambda)(\sigma\mu_x\mu_y + \phi_p(1,0,0) - \lambda) - (\mu_y + \beta_y\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0))\phi_y(1,0,0).$$

Let $z = \lambda - \mu_x$. To show that $z < 0$, we first obtain the following characteristic polynomial in terms of the new variable, z :

$$(\mu_y - \phi_y(1,0,0) - z - \mu_x)(\sigma\mu_x\mu_y + \phi_p(1,0,0) - z - \mu_x) - (\mu_y + \beta_y\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0))\phi_y(1,0,0).$$

This corresponds to the characteristic polynomial of the following 2×2 matrix:

$$\overline{J} = \begin{bmatrix} \mu_y - \phi_y(1,0,0) - \mu_x & \mu_y + \beta_y\mu_x\mu_y - \sigma\mu_x\mu_y - \phi_p(1,0,0) \\ \phi_y(1,0,0) & \sigma\mu_x\mu_y - \mu_x + \phi_p(1,0,0) \end{bmatrix}$$

Notice that the trace of $\overline{J}$ is $tr(\overline{J}) = \mu_y - \phi_y(1,0,0) - 2\mu_x + \sigma\mu_x\mu_y + \phi_p(1,0,0)$. By standard criteria, the eigenvalues have negative real parts if and only if $\det(\overline{J}) > 0$. That is,

$$(\mu_x(1-\sigma\mu_y)-\phi_p(1,0,0))(\mu_x+\phi_y(1,0,0)-\mu_y)-(\mu_y+\beta_y\mu_x\mu_y-\sigma\mu_x\mu_y-\phi_p(1,0,0))\phi_y(1,0,0) > 0 \text{ and}$$

$$\mu_x^2-\mu_x(\mu_y-(\frac{(1-\beta_y\mu_y)\phi_y(1,0,0)-\phi_p(1,0,0)}{(1-\sigma\mu_y)}))+\frac{\mu_y(\phi_p(1,0,0)-\phi_y(1,0,0))}{(1-\sigma\mu_y)} > 0.$$

The corresponding equality is a quadratic equation in μ_x with real solutions provided the discriminant $\Delta_x \geq 0$. On solving the inequality for positive values of μ_x, we obtain that we need

$$\mu_x > \frac{([\mu_y(1-\sigma\mu_y)-(1-\beta_y\mu_y)\phi_y(1,0,0)-\phi_p(1,0,0)])}{2(1-\sigma\mu_y)}+$$

$$\frac{\sqrt{[\mu_y(1-\sigma\mu_y)-(1-\beta_y\mu_y)\phi_y(1,0,0)-\phi_p(1,0,0)]^2-4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0)-\phi_y(1,0,0))}}{2(1-\sigma\mu_y)}.$$

Consequently, large μ_x value forces a negative value of $tr(\overline{J})$, and hence imply the stability of $[1,0,0]$. We now state a summary of these results on the stability of the trivial equilibrium solutions.

Theorem 5.1. *System (1) always has two geometric trivial solutions at*

$$[(\mu_x)^t, 0, 0] \, and \;\; [0, (\mu_y)^t, 0].$$

If

$$\mu_x < \frac{([\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)])}{2(1-\sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)]^2 - 4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0) - \phi_y(1,0,0))}}{2(1-\sigma\mu_y)}$$

and

$$\mu_y < \frac{([\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)])}{2(1-\sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)]^2 - 4\mu_x(1-\sigma\mu_x)(\phi_p(0,1,0) - \phi_x(0,1,0))}}{2(1-\sigma\mu_x)}$$

then a stable, positive nontrivial geometric solution exists. Moreover, if

$$\mu_x > \frac{([\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)])}{2(1-\sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)]^2 - 4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0) - \phi_y(1,0,0))}}{2(1-\sigma\mu_y)}$$

then $[(\mu_x)^t, 0, 0]$ *is stable,* $[0, (\mu_y)^t, 0]$ *is unstable and there is no positive nontrivial geometric solution. Also, if*

$$\mu_y > \frac{([\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)])}{2(1-\sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)]^2 - 4\mu_x(1-\sigma\mu_x)(\phi_p(0,1,0) - \phi_x(0,1,0))}}{2(1-\sigma\mu_x)}$$

then $[(\mu_x)^t, 0, 0]$ *is unstable,* $[0, (\mu_y)^t, 0]$ *is stable and there is no positive nontrivial geometric solution, where* $\Delta_x, \Delta_y \geq 0$.

6. Application

To apply our general results to a specific model, we consider System (1) with

$$G(x, y, p) = \frac{p}{y+p},$$

where (x, y, p) belong to the set

$$\Omega := \{(x, y, p) \mid 0 \leq \frac{x}{y} \leq \frac{y+p}{y}\}.$$

Then

$$H(x, y, p) = 1 - \frac{x}{(y+p)}$$

and

$$\phi(x, y, p) = \frac{\mu_x x y}{y + p}.$$

If $\mu_x = \mu_y = \beta_x = \beta_y = \sigma$, the Characteristic Equation (11) has a positive real solution at

$$\lambda^* = \frac{\sigma[2 + \sigma^2(1 - \sigma^2)] + \sigma^3\sqrt{4 + (1 - \sigma^2)^2}}{2(1 - \sigma^2)},$$

while System (15) has a unique positive fixed point at

$$[x_0, y_0, p_0] = [\frac{(1 - \sigma^2) + \sqrt{4 + (1 - \sigma^2)^2}}{2}, \frac{(1 - \sigma^2) + \sqrt{4 + (1 - \sigma^2)^2}}{2}, 1] \in \Omega.$$

To establish conditions for the stability of the trivial equilibrium solutions, we note that

$$\begin{aligned}
\phi_x(1,0,0) &= \phi_y(1,0,0) = \phi_y(0,1,0) = \phi_p(1,0,0) = \phi_p(0,1,0) = 0, \\
\phi_x(0,1,0) &= \mu_x, \ \Delta_x \geq 0 \text{ and } \Delta_y \geq 0.
\end{aligned}$$

All the conditions of Theorem 5.1 are satisfied using the above partial derivatives provided that

$$0 \leq \frac{x_0}{y_0} \leq \frac{y_0 + p_0}{y_0}.$$

7. Conclusion

In this article we extend the pair-formation models of Kendall [24], Keyfitz [25], Fredrickson [11], Pollard [36] and Hadeler *et al.'s* [13-18] to populations with discrete non-overlapping generations. The results on existence and stability of geometric solutions parallel those of Hadeler *et al.* even for the case when the marriage function ϕ is a function of p, the population size of pairs. The development and analysis of our discrete, nonlinear pair-formation model with nonoverlapping generations allows for the possibility of not only studying the population dynamics of populations with discrete non-overlapping generations but also of incorporating population genetics at the level of the individual. Here, we have a framework where we can look at the consequences of mating on the genotypic or phenotypic composition of a population of individuals. The prior work of Castillo-Chavez *et al. [7]* suggests that a key component (in the absence of selection) on the impact of mating functions on the long-term genotypic or phenotypic composition of a population is given by the degree of the difference among the rates of pair-dissolution for the types involved. We are currently exploring this possibility. Our formalism also allows for the exploration of mating systems on population with complex (chaotic) dynamics. In fact, when $\mu = \mu_x = \mu_y$,

$$T(t+1) = F(p(t)) + \mu T(t),$$

Hence, the exploration of the role of various forms for F on the dynamics of a two-sex population presents an interesting class of mathematical problems for systems of nonlinear difference equations. We have just began to explore these possibilities. The results are quite different as, of course, homogeneity no longer holds.

The development of a two-sex framework for modeling systems of mating for populations with discrete non-overlapping generations offers the possibility of looking at the impact of gender on the population dynamics of a multitude of biological systems. Current mathematical studies in the field of population biology are based on simple one-sex models. Whether or not prior theoretical results for one-sex models hold in two-sex populations is a question that needs to be examined. We hope that this reformulation of the work of Hadeler *et al.* in this setting would provide a starting point.

8. Appendix

Proof of Lemma 3.1: Since $\phi : [0,\infty) \times [0,\infty) \times [0,\infty) \to [0,\infty)$ then $\beta_x\mu_x\mu_y + \mu_x - \lambda > 0$ whenever $\lambda - \mu_x > 0$. Hence, $\frac{\beta_x\mu_x\mu_y}{\lambda-\mu_x} - 1 > 0$. Also, $\beta_y\mu_y\mu_x + \mu_y - \lambda > 0$ whenever $\lambda - \mu_y > 0$. Hence, $\frac{\beta_y\mu_y\mu_x}{\lambda-\mu_y} - 1 > 0$. Therefore, if $\lambda > \max\{\mu_x, \mu_y\}$ and $\lambda < \min\{\beta_x\mu_x\mu_y + \mu_x, \beta_y\mu_y\mu_x + \mu_y\}$ then $\frac{\beta_x\mu_x\mu_y}{\lambda-\mu_x} - 1 > 0$ and $\frac{\beta_y\mu_y\mu_x}{\lambda-\mu_y} - 1 > 0$. We define $\lambda_{\text{min}} = \max\{\mu_x, \mu_y\}$ and $\lambda_{\text{max}} = \min\{\beta_x\mu_x\mu_y + \mu_x, \beta_y\mu_y\mu_x + \mu_y\}$. Equation (11) has no solution whenever $\lambda_{\text{min}} > \lambda_{\text{max}}$. Hence, we consider only the case when $\lambda_{\text{min}} < \lambda_{\text{max}}$. We search for solutions to Equation (11) where $\lambda_{\text{min}} < \lambda_{\text{max}}$ and λ is in the open interval $(\lambda_{\text{min}}, \lambda_{\text{max}})$.

As λ increases, the left-hand-side of Equation (11) increases while the right-hand-side decreases from a non-negative value $C \in [0, \infty]$, where $C = \phi(\frac{\beta_x\mu_x\mu_y}{\lambda_{\text{min}}-\mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda_{\text{min}}-\mu_y} - 1, 1) \leq \infty$. Consequently, Equation (11) has a unique solution, if and only if,

$$C > -\sigma\mu_x\mu_y + \lambda. \qquad (12)$$

In order to obtain specific conditions the following approximations are used. For x large enough ($x \to \infty$), $\phi(x,y,1) = x\phi(1,\frac{y}{x},\frac{1}{x}) \approx x[\phi(1,0,0)+\phi_y(1,0,0)\frac{y}{x}+\phi_p(1,0,0)\frac{1}{x}] = y\phi_y(1,0,0)+\phi_p(1,0,0)$. Therefore,

$$\phi(x,y,1) \approx \begin{cases} y\phi_y(1,0,0)+\phi_p(1,0,0) & \text{as } x \to \infty \\ x\phi_x(0,1,0)+\phi_p(0,1,0) & \text{as } y \to \infty. \end{cases}$$

$$\text{As } \lambda_{\min} \to \mu_x^+, \frac{\beta_x\mu_x\mu_y}{\lambda_{\min}-\mu_x} - 1 \to +\infty$$

and

$$\phi(\frac{\beta_x\mu_x\mu_y}{\lambda_{\min}-\mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda_{\min}-\mu_y} - 1, 1) \approx (\frac{\beta_y\mu_y\mu_x}{\mu_x-\mu_y} - 1)\phi_y(1,0,0)+\phi_p(1,0,0).$$

Similarly,

$$\text{as } \lambda_{\min} \to \mu_y^+, \frac{\beta_y\mu_y\mu_x}{\lambda_{\min}-\mu_y} - 1 \to +\infty$$

and

$$\phi(\frac{\beta_x\mu_x\mu_y}{\lambda_{\min}-\mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda_{\min}-\mu_y} - 1, 1) \approx (\frac{\beta_x\mu_x\mu_y}{\mu_y-\mu_x} - 1)\phi_x(0,1,0)+\phi_p(0,1,0)).$$

Therefore,

$$C \approx \begin{cases} \frac{\beta_y\mu_y\mu_x - \mu_x + \mu_y}{\mu_x - \mu_y}\phi_y(1,0,0) + \phi_p(1,0,0) & \text{as } \lambda_{\min} \to \mu_x^+, \\ \frac{\beta_x\mu_x\mu_y - \mu_y + \mu_x}{\mu_y - \mu_x}\phi_x(0,1,0) + \phi_p(0,1,0) & \text{as } \lambda_{\min} \to \mu_y^+. \end{cases}$$

If $\lambda_{\min} \to \mu_x^+$ then Equation (12) implies that

$$(\frac{\beta_y\mu_y\mu_x}{\mu_x - \mu_y} - 1)\phi_y(1,0,0) + \phi_p(1,0,0) > -\sigma\mu_x\mu_y + \mu_x$$

where $\mu_x > \mu_y$. Hence, if the discriminant

$$\Delta_x = [\mu_y(1-\sigma\mu_y)-(1-\beta_y\mu_y)\phi_y(1,0,0)-\phi_p(1,0,0)]^2-4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0)-\phi_y(1,0,0)) \geq 0,$$

then

$$\mu_x < \frac{([\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)])}{2(1-\sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1-\sigma\mu_y) - (1-\beta_y\mu_y)\phi_y(1,0,0) - \phi_p(1,0,0)]^2 - 4\mu_y(1-\sigma\mu_y)(\phi_p(1,0,0) - \phi_y(1,0,0))}}{2(1-\sigma\mu_y)}.$$

Similarly, if the discriminant

$$\Delta_y = [\mu_x(1-\sigma\mu_x)-(1-\beta_x\mu_x)\phi_x(1,0,0)-\phi_p(1,0,0)]^2-4\mu_x(1-\sigma\mu_x)(\phi_p(1,0,0)-\phi_x(1,0,0)) \geq 0,$$

then

$$\mu_y < \frac{([\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)])}{2(1-\sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1-\sigma\mu_x) - (1-\beta_x\mu_x)\phi_x(0,1,0) - \phi_p(0,1,0)]^2 - 4\mu_x(1-\sigma\mu_x)(\phi_p(0,1,0) - \phi_x(0,1,0))}}{2(1-\sigma\mu_x)}.$$

These two last inequalities give the necessary and sufficient conditions for existence of non-trivial geometric solutions. These solutions would have positive eigenvectors $(x_0, y_0, p_0) \in \Omega$.

Proof of Theorem 4.1: Let $\lambda \neq \frac{\lambda^*}{\lambda^* + L(BV)}$ be the eigenvalue of $J(w_0)$ with corresponding eigenvector V. Then $J(w_0)V = \lambda V$. Using Equation (20) we obtain $\frac{BV - w_0 L(BV)}{\lambda^* + L(BV)} = \lambda V$. Now, we show that $v = V + \frac{1}{\lambda(\lambda^* + L(BV)) - \lambda^*} w_0 L(BV)$ is an eigenvector of B, corresponding to the eigenvalue $\lambda(\lambda^* + L(BV))$.

$$\begin{aligned} Bv &= BV + \tfrac{\lambda^* w_0 L(BV)}{\lambda(\lambda^* + L(BV)) - \lambda^*} \\ &= \lambda V(\lambda^* + L(BV)) + w_0 L(BV) + \tfrac{\lambda^* w_0 L(BV)}{\lambda(\lambda^* + L(BV)) - \lambda^*} \\ &= \lambda V(\lambda^* + L(BV)) + \tfrac{w_0 L(BV)}{\lambda(\lambda^* + L(BV)) - \lambda^*}(\lambda(\lambda^* + L(BV)) - \lambda^* + \lambda^*) \\ &= \lambda(\lambda^* + L(BV))v. \end{aligned}$$

Conversely, if $\lambda \neq \lambda^*$ is an eigenvalue of B corresponding to an eigenvector v, we show that $\frac{\lambda}{\lambda^* + L(BV)}$ is an eigenvalue of $J(w_0)$ corresponding to an eigenvector $V = w_0 - v$ [that is, $J(w_0)V = \frac{\lambda}{\lambda^* + L(BV)} V$]. Using Equation (20) and the fact that

$V = w_0 - v$ and $L(w_0) = L(v) = 1$, we obtain that

$$\begin{aligned} J(w_0)V &= \frac{BV - w_0 L(BV)}{\lambda^* + L(BV)} \\ &= \frac{Bw_0 - Bv - w_0 L(Bw_0 - Bv)}{\lambda^* + L(BV)} \\ &= \frac{Bw_0 - Bv - \lambda^* w_0 L(w_0) + \lambda w_0 L(v)}{\lambda^* + L(BV)} \\ &= \frac{-\lambda v + \lambda w_0}{\lambda^* + L(BV)} \\ &= \frac{\lambda}{\lambda^* + L(BV)} V = \frac{\lambda}{2\lambda^* - \lambda} V. \end{aligned}$$

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